Decomposition of natural litter mixtures in a deciduous forest[1]

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Decomposition rates were measured for four litter mixtures, including mixed species and ages, representing common herbaceous litter and canopy leaf litter in a Canadian deciduous forest. Quantitative changes were expressed as monthly exponential weight loss rates based on measurements from a 6-month and from a 16-month period. Monthly loss rates of herbaceous litter were up to 11 times those of mixed-age canopy leaf mixtures (calculated over 6 months), and the loss rate for mixed-age canopy leaf litter calculated over 6 months was more than 3 times that monitored over 16 months. Similarly, qualitative changes, estimated as monthly arithmetic organic loss and lignin gain rates, were generally more rapid for herbaceous litter than for canopy litter, and mixed-age canopy litter had a faster rate of change calculated over 6 months compared with that estimated over the 16-month period. Following the initial rapid release of nutrients, decomposition slows and becomes more dependent on the availability and distribution of decomposer organisms. We hypothesize that an undisturbed litter layer provides the microenvironments required by these decomposers and that a spatial variability in decomposition therefore arises only as a result of spatial variability in litter distribution or disturbance (e.g., by wind) of the litter layer.

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Les auteurs ont mesuré les taux de décomposition de quatre mélanges de litières, comprenant des mélanges d'espèces et des mélanges de litières d'âges différents (inéquiennes), et représentant des espèces herbacées et des espèces de la voute foliaire d'une forêt décidue canadienne. Les changements quantitatifs sont exprimés par les taux mensuels exponentiels de perte de poids, évalués à partir de mesures prises pendant une période de 6 mois et une période de 16 mois. Pour la litière de plantes herbacées, les taux mensuels de perte de poids, sur une période de 6 mois, sont jusqu'à 11 fois plus élevés que pour les mélanges inéquiennes de feuilles de la voute foliaire; pour ces dernières, le taux de perte de poids sur 6 mois est plus de 3 fois plus élevé que s'il est calculé sur une période de 16 mois. Pareillement, les changements qualitatifs (estimés par les taux arithmétiques mensuels de perte de matière organique et de gain de lignine) sont généralement plus rapides pour la litière herbacée que pour la litière de la voute foliaire, et la litière inéquienne de la voute foliaire présente des taux de changement plus élevés si ceux-ci sont calculés sur une période de 6 mois que s'ils sont estimés sur une période de 16 mois. Après une libération initiale rapide d'éléments nutritifs, la décomposition ralentit et devient plus étroitement dépendante de la disponibilité et de la répartition des organismes décomposeurs. Nous émettons l'hypothèse qu'une couche non perturbée de litière fournit aux organismes décomposeurs les micro-environnements que ceux-ci exigent et que, par conséquent, les variations de la décomposition sont dues seulement à la variation spatiale dans la répartition et la perturbation (par exemple, par le vent) de la couche de litière.

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Introduction

Nutrient cycling in wooded ecosystems is dependent on litter fall and subsequent decomposition. This decomposition releases nutrients from their temporary storage in plant biomass, and the rate of this release determines the availability of nutrients for future plant growth and development.

Most studies have reported on decomposition of litter artificially composed to contain only the leaves of a single species. These experiments lack reality in that the tissues, the chemical decomposition products, and the decomposer microenvironments all lack their normal heterogeneity. Of course this is necessary to reduce the variability of decomposition rates, the objective of such studies. However, because homogeneous litter seldom occurs, and systematic methods do not exist to apportion rates for single species throughout the mixture of litter which normally exists on the floor, applying rates derived from studies of single species litter is very difficult. An alternate approach has been used in comparing the decomposition rates of mixed-species litter among several communities in the Great Dismal Swamp (Day 1982). Samples were composed containing leaves of several species in approximately the same proportion as on the forest floor; these mixed samples were found to represent each community more accurately than any series of samples containing only a single species.

An earlier study of our deciduous woodlot indicated that the floor was not homogeneous but had mesoscale rises and depressions, each about 1 m in diameter with a 0.5-m vertical maximum. This topography produced "patches" characterized by different litter mixtures, physical conditions, microbial populations, and ultimately different decomposition rates (Dwyer and Merriam 1981). The present study was designed to investigate the potential decay rates of these litter mixtures when they were moved to a common homogeneous site and other "patch-specific" factors were eliminated. Because most of the naturally occurring litter mixtures were complex, changes were more difficult to analyze than those of single litter types, but these mixtures were necessary if the physical environment provided and microbial populations supported by the litter mixtures were to be comparable with those found on the woodlot floor.

Decomposition rates of four litter mixtures common to a deciduous woodlot were compared over a single season (6 months). One of the mixtures, a combination of intact and aged beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) leaves, was also monitored for 16 months to measure changes occurring in the second season. The litter mixtures were chosen to represent common naturally occurring combinations of litter species at both early and advanced stages of decay. Therefore the decomposition rates which we measured are applicable to litter mixtures which accumulate natu-

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rally on homogeneous mesoscale sites of the forest floor.

Study site

Six level sites about 1 m in diameter were selected within a 13-ha beech–maple woodlot located south of Ottawa (Dwyer and Merriam 1981) to serve as homogeneous sites for the experiment. The canopy layer is dominated by beech and sugar maple with a few basswood (*Tilia americana* L.) and ironwood (*Ostrya virginiana* (Mill.) K. Koch). The middle stratum is open with the exception of occasional beech and maple saplings. Ground vegetation is seasonal. In early spring, leeks (*Allium tricoccum* Ait.) are prevalent and are concentrated in the drier elevated areas where they cover approximately 31% of the ground. In the few weeks before full canopy closure many ephemeral herbs appear; they are detailed elsewhere (Merriam et al. 1982). As canopy closes, most of the herbs produce seeds and their vegetative parts begin to decompose. By late July, blue cohosh (*Caulophyllum thalictroides* (L.) Michx.) is the dominant herbaceous plant, and it is concentrated in more protected depressions where it covers 14% of the ground. Canopy litter falls evenly over the whole woodlot floor, mainly in October, but by the following spring it has been moved into the topographic depressions (Merriam et al. 1982).

Materials and methods

Four litter mixtures (each replicate weighing 3.0 g dry weight) were examined during a 6-month decay period extending from May to November. Litter, which was limited to leaf material, was collected from the woodlot floor surrounding the study plot in late October and during the last week of the following April. Mixtures were a 1:1 combination of intact beech and maple leaves collected in the spring just before the experiment began (Be–Ma); a 1:1 combination of cohosh leaves and stems collected the previous fall and air dried (cohosh); fresh leek leaves collected just prior to the experiment (leek); and a combination of one-third intact beech leaves, one-third intact maple leaves, and one-sixth each aged beech and maple leaves, all collected in the spring just before the 6-month experiment began (mixed-age Be–Ma). Intact leaves showed no visible signs of decay, whereas aged leaves were filamentous and lacked the fleshy matrix on 25% or more of their surface area.

For the 16-month experiment, an additional litter mixture, identical with that designated "mixed-age Be–Ma" but with leaves collected in late May, was monitored from July to November of the next year.

Decay rates of litter mixtures were measured in mesh bags. The mesh-bag technique has become a standard method of confining leaf litter and estimating decomposition rate of various litter species under a range of environmental conditions (Crossley and Hoglund 1962; Witkamp 1966; Gosz et al. 1973; Macauley 1975; Fogel and Cromack 1977; Vossbrinck et al. 1979). Selection of mesh size restricts access by decomposer species and influences processes involved in decomposition (Anderson 1973). Fragmentation can cause weight loss from litter bags, but generally only leaching and invertebrate and microbial degradation selectively remove litter components resulting in qualitative or chemical changes to the litter.

Bags were made from 2 × 1 mm flexible fibreglass reinforcing mesh (Flintkote 990-06), sewn with heavy polyester thread. Each bag was constructed so the bottom (15 × 15 cm) lay flush against the ground; the top was then cut larger than the bottom and "pleated" so that even when full of leaves the bag did not curl away from the ground. Surface litter was cleared and the bag edges were anchored with stovepipe wire staples so that good contact was maintained between the bags and soil surface. Before inclusion in mesh bags, all air-dried leaves were remoistened in a high humidity. Forty-two replicate bags of each mixture monitored during the 6-month period and an additional 66 replicate bags of the mixture monitored during the 16-month period (each containing 3.0 g dry weight) were randomly located among the six level areas of the woodlot floor.

At each sample period (0, 2, 3, 4, 5, and 6 months into the 6-month experiment and 0, 3, 4, 5, 9, 10, 14, 15, and 16 months into the 16-month experiment) at least six bags were randomly selected and removed from each set of replicates. They were sealed in plastic bags to maintain field moisture content and stored at −5 to −10°C before analysis.

Analysis began by air drying, weighing, and then grinding the contents of each bag in a Wiley mill to pass through screen size No. 40 (0.420 mm). Subsamples (0.25 g) from most bags were used for organic matter determination (Paine 1971) and additional 0.50-g subsamples were analyzed for lignin content (Van Soest 1963).

Weight loss through time was noted to estimate decomposition. Weight loss as a function of decay is often represented by a linear regression on a semilogarithmic plot (Olson 1963; Schlesinger 1977). A least-squares regression on plots of the natural logarithm of percent of litter weight remaining over time was used to determine the best linear model of the decomposition process for each litter mixture and decay period studied. Arithmetic regressions were calculated for organic loss and lignin gain. All data sets were tested for autocorrelation using the Durbin–Watson statistic (Wesolowsky 1976).

All regression slopes were tested using the F statistic to indicate whether the individual decay rates differed significantly from zero. The difference in slope of decay curves for the various 6-month litter mixtures was tested by a simple regression technique using the original data, a more powerful method than comparing the regression coefficients of the calculated lines (Draper and Smith 1966). The differences between mean empircal values used to plot the two decay curves at each time interval were calculated and plotted over time. If the slope of the regression line passing through these mean differences was found to be significantly greater than zero ($P < 0.10$), it was concluded that the slopes of the original two lines were different. Since data from 6-month and 16-month decay curves could not be paired, their slopes were compared using a t-test.

Results and discussion

Quantitative decomposition measures

Table 1 shows the weight loss of all litter mixtures during a 6-month summer decay period and of "mixed-age Be–Ma" litter during a 16-month decay period. Four observations can be made. Most obvious is the rapid rate of weight loss of leek leaves; the second fastest rate of loss is for blue cohosh leaves and stems, although it is not significantly faster than the 6-month loss rate from "mixed-age Be–Ma" litter ($P > 0.10$). Weight loss from "mixed-age Be–Ma" averaged over 6 months is more rapid than weight loss from the same mixture averaged over 16 months, and finally, rate of weight loss is fastest for the first 4 months of the 16-month period and slowest for the last 6 months. Except where noted (Table 1), all comparisons are statistically different ($P < 0.10$).

Rapid weight loss by herbaceous leaves has been documented (Shanks and Olson 1961; Kuhnelt 1969). The speed of decomposition of leek and cohosh leaves in this study was also verified by several seasons of field observations. Leek leaves were collected while still green because they were unidentifiable by the time canopy trees leafed; cohosh material was collected in the fall, air dried, and stored over the winter because it was impossible to distinguish cohosh leaves on the woodlot floor in spring. In fact, the decay rate listed for cohosh leaves and stems in Table 1 is much lower than for leaves alone; at the end of the 6-month period it was rare to find anything but stems remaining in "cohosh" decay bags.

Our results show the significance of early leaching from a deciduous litter that is subjected to cold snowy winters. The loss rate for mixed-age beech and maple litter (mixed-age Be–Ma) measured over 6 months begun in May was more than 3 times that measured over a 16-month period begun in July. Rapid early weight loss followed by slower losses is a pattern seen in many decomposition studies. However, most studies

TABLE 1. Monthly litter decomposition rates measured as weight loss for four litter mixtures

Decay period	% litter weight at start of period	Litter mixture	Exponential weight loss rate	Correlation coefficient (*R*)	Rate comparison**	Durbin–Watson statistic
May–November (6 months)	100	Be–Ma	−0.0469*	0.81(*N*=42)		1.570***
		Cohosh	−0.0804*	0.84(*N*=42)		1.784***
		Leek	−0.6409*	0.80(*N*=42)		1.178
		Mixed-age Be–Ma	−0.0561*	0.77(*N*=42)		1.366***
July–November (first 4 months)	100	Mixed-age Be–Ma	−0.0463*	0.87(*N*=30)		1.702***
May–November (last 6 months)	84.2	Mixed-age Be–Ma	−0.0168*	0.60(*N*=30)		2.186***
July–November (total 16 months)	100	Mixed-age Be–Ma	−0.0154*	0.78(*N*=60)		1.189

NOTE: *, slopes differ significantly from zero ($P < 0.01$); **, all comparisons significantly different ($P < 0.10$) except those noted here; ***, no significant autocorrelation ($P < 0.01$).

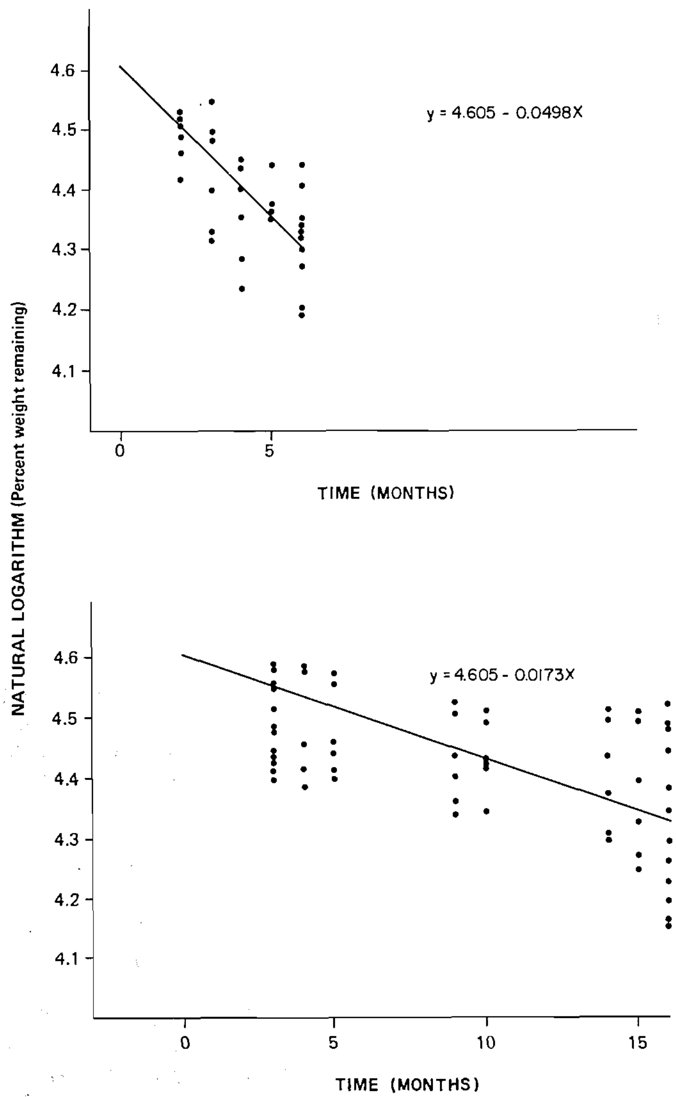

FIG. 1. Rate of litter decomposition (measured as weight loss) for mixed-age beech–maple litter over 6 months and 16 months. Note the slipped x-axis to visually line up comparable months.

have been in areas of mild winters, whereas litter in this study was subjected to effects of freezing and to sudden and intensive spring leaching caused by snow melt (mean December–March air temperature, −7.7°C; mean snowfall, 44.8 cm (Anonymous 1982)). Under these conditions the potential for rapid leaching is great during and immediately following spring melt and also is important between leaf fall and freeze-up.

Figure 1 shows a rapid weight loss, attributed to leaching, dominating all of the 6-month period (May to November) and the first 4 months of a 16-month period (July to November). The slightly slower monthly decay rate for the first 4 months of the 16-month period (Table 1) may be attributed to the fact that this experiment was not exposed to the spring leaching period, although there is no significant difference ($P > 0.10$) between the weight loss rate of "mixed-age Be–Ma" litter during the 6-month period and the first 4 months of the 16-month experiment. Intact leaves containing readily soluble substrates would undergo some leaching during summer rains and much more during the fall leaching period. The significantly lower ($P < 0.10$) overall rate for the 16-month period is a reflection of slower decomposition processes which followed the relatively rapid weight loss of the first season. Because the slope of the regression line was determined by its goodness of fit throughout the 16-month period, the initial rapid weight loss was reduced in importance and the overall slope decreased accordingly.

Statistical comparison of decay curves followed strict criteria. As mentioned earlier, comparison of regression slopes required a pairing of observations. Since several replicates were sampled at each time interval and there was no logical method of pairing replicate measurements from two decay curves, a mean was calculated for each time interval and only these means were paired for comparison of regression slopes using F and t statistics. This resulted in a severe reduction in data points (and degrees of freedom) used in statistical testing, even though each curve was based on information from all data points. We therefore feel that results of our statistical analysis (Tables 1 and 2) represent a very conservative interpretation of the data.

Our canopy litter mixtures represent natural mixed species litter at early and advanced stages of decay. Monthly decay

TABLE 2. Monthly litter decomposition rates measured as organic loss and lignin gain for four litter mixtures

Decay period	Litter mixture	Arithmetic organic loss rate	Correlation coefficient (R)	Rate comparison **	Durbin–Watson statistic	Arithmetic lignin gain rate	Correlation coefficient (R)	Rate comparison **	Durbin–Watson statistic
May–November (6 months)	Be–Ma	−1.83*	0.62(N=36)		1.314***	0.99*	0.59(N=15)		2.718***
	Cohosh	−1.90*	0.69(N=36)		1.844***	1.62*	0.72(N=15)		1.927***
	Mixed-age Be–Ma	−1.54*	0.72(N=36)		2.015***	0.85*	0.65(N=15)		1.576***
July–November (first 4 months)	Mixed-age Be–Ma	−1.36*	0.72(N=30)		2.466***	0.30*	0.50(N=30)		1.478***
July–November (total 16 months)	Mixed-age Be–Ma	−1.02*	0.48(N=66)		1.491***	0.25*	0.42(N=65)		1.660***

NOTE: *, slopes differ significantly from zero ($P < 0.01$); **, all comparisons significantly different ($P < 0.10$) except those noted here; ***, no significant autocorrelation ($P < 0.01$).

rates are therefore difficult to compare with single-species weight losses common in the literature. Anderson (1973) calculated an average monthly decay constant over a 13-month period of −0.00047 for intact beech leaves confined in bags in an English woods (mesh size 175 μm). Table 1 shows faster decay rates for litter confined in our bags with a substantially larger mesh size of 1 × 2 mm. We suggest that the faster rates we monitored were a result of the greater accessibility of our bagged litter to invertebrates (Edwards and Heath 1963) and increased fragmentation losses. Gosz et al. (1973) obtained comparable monthly rates over an 11-month period of −0.0300 for sugar maple and −0.0245 for beech leaves, and Mellilo et al. (1982) measured annual decomposition rates of −0.25 for sugar maple and −0.08 for beech leaves. These estimates reflect considerable variation from one study to another despite the concentration on single species. This variation may be due to differences in litter collection methods or in the duration and severity of the winter period.

Since decomposition was monitored as a function of time, there was some concern about autocorrelation. Table 1 indicates most data sets were free of autocorrelation. In interpreting sets with a borderline Durbin–Watson statistic we feel that our experimental method, which precluded using any litter sample to generate more than one of the data points, minimized the risk of the statistical dependence of errors on preceding errors.

Qualitative decomposition measures

Qualitative changes in decomposing litter were reflected in arithmetic organic loss rates and lignin gain rates (Table 2). Organic analysis (loss on ignition) facilitated comparison of the organic component of litter through time without consideration of the ash fraction. Lignin was also analyzed because it is known to be a resistant constituent of litter (Peevy and Norman 1948; Pinck et al. 1950; Christensen 1973) and it has more recently been suggested as an index of decay (Cromack 1973; Meentemeyer 1978; Melillo et al. 1982). Lignin is decomposed mainly in soil and lower litter layers (Peevy and Norman 1948) and is not significantly broken down in litter bags. Therefore, loss of the more soluble and easily decomposable organic materials from bags increases the lignin proportion of remaining litter.

Qualitative analyses among replicates were more variable than quantitative measures and few comparisons were statistically different using the conservative tests described earlier, but several points can be made from Table 2. First, the arithmetic organic loss and lignin gain rates for leeks are absent; weight loss was so rapid that insufficient sample remained for qualitative analyses (only 2% of starting material was left after 3 months). The other herbaceous mixture (cohosh) showed the most rapid qualitative change, followed by the intact canopy mixture (Be–Ma) which was in turn followed by the mixed-age canopy mixture (mixed-age Be–Ma), all measured over 6 months. The slowest rates of all were recorded for "mixed-age Be–Ma" monitored over the 16-month period.

This pattern for qualitative change is the same as that for weight loss with the exception that the intact canopy mixtures did not have a faster rate of weight loss than mixed-age canopy litter monitored over 6 months, indicating that qualitative changes may not have been reflected in a weight loss. In fact, differences in lignin gain rates among canopy mixtures were largely due to differences in initial lignin concentrations; "mixed-age Be–Ma" litter was about 6.5% higher in lignin than "Be–Ma" litter at the start of the 6-month period. This more resistant material underwent further decomposition more slowly than did the intact litter in the "Be–Ma" mixture and so its rate of lignin gain was lower (+0.85 compared with +0.99).

Conclusion

These mixed-litter experiments were carried out on homogeneous sites of the forest floor, but the observed differences in decay rates among mixtures are the basis of spatial variability in the decomposition process. Quantitative and qualitative changes in early stages of canopy leaf decomposition and throughout most stages of herbaceous litter decay are rapid, and it is suggested that they are mainly the result of physical leaching and some abiotic fragmentation. These processes occur anywhere on the woodlot floor. Therefore, there is no spatial variability in nutrient release except that caused by spatial distribution of herb growth. However, changes later in decomposition are slower and likely more dependent on chemical degradation by microbial and invertebrate decomposer organisms, which vary in distribution and abundance according to availability of their specific habitat requirements. These requirements may be provided by the micronutrients generated in the decaying litter mixtures themselves, if undisturbed. For example, in an earlier study we found that leaf litter was windswept from rises and accumulated in topographic hollows (Dwyer and Merriam 1981; Merriam et al. 1982). These topo-

graphic hollows provided the physical and resource requirements for decomposers and the more resistant compounds concentrated in aged or partially decayed litter were decomposed there. In the present experiment litter was confined in bags on homogeneous level sites. These undisturbed litter mixtures underwent an initial rapid nutrient release and those with more resistant compounds also underwent slower decay processes. Thus, we feel there is evidence that the physical and resource requirements of microbial and invertebrate decomposers are provided by the microenvironment of the decaying litter mixtures themselves. We therefore hypothesize that all sites with an accumulation of surface litter have a potential for complete decomposition, and spatial variability in the decomposition process arises only from spatial variability in litter distribution.

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